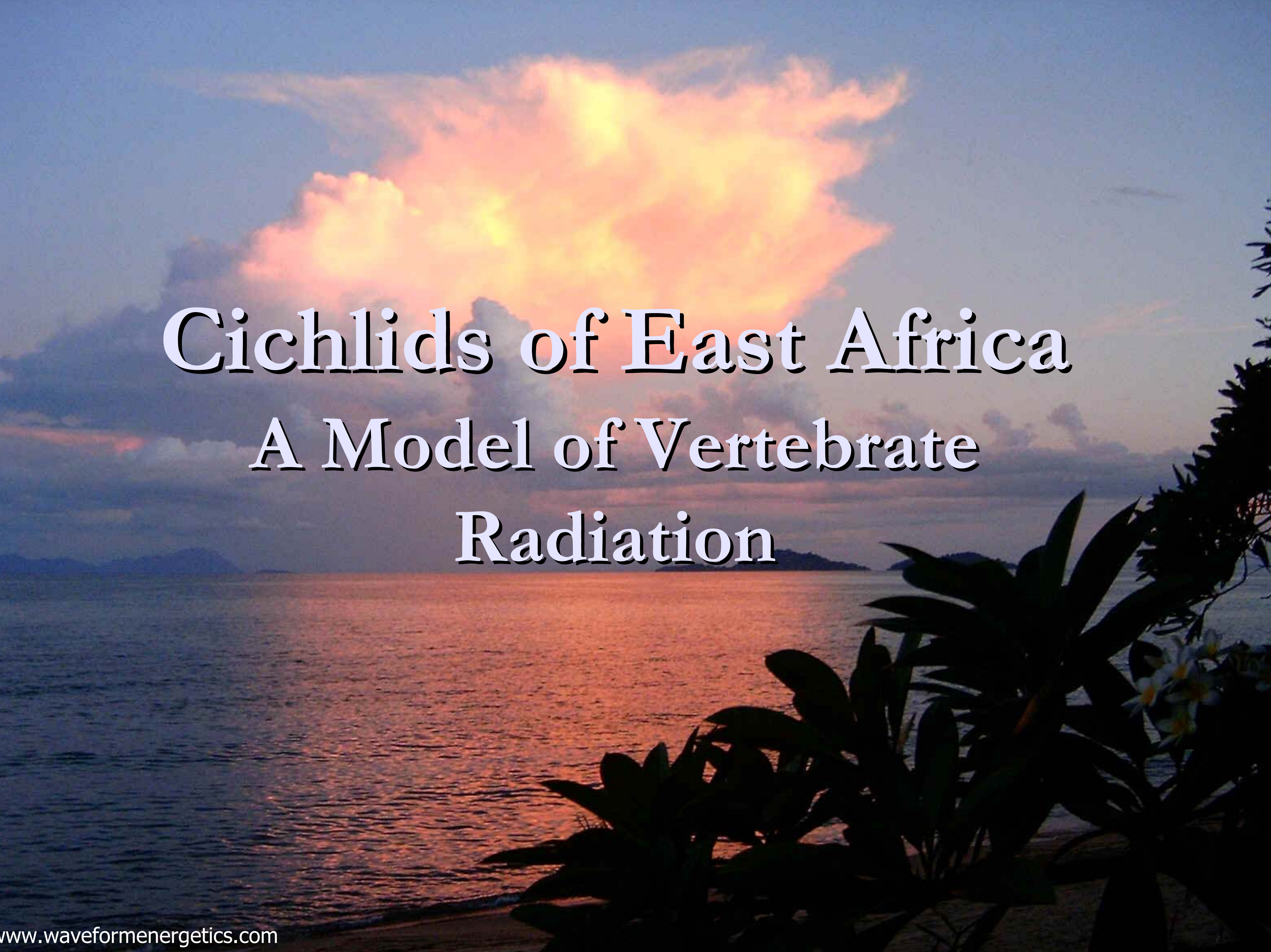
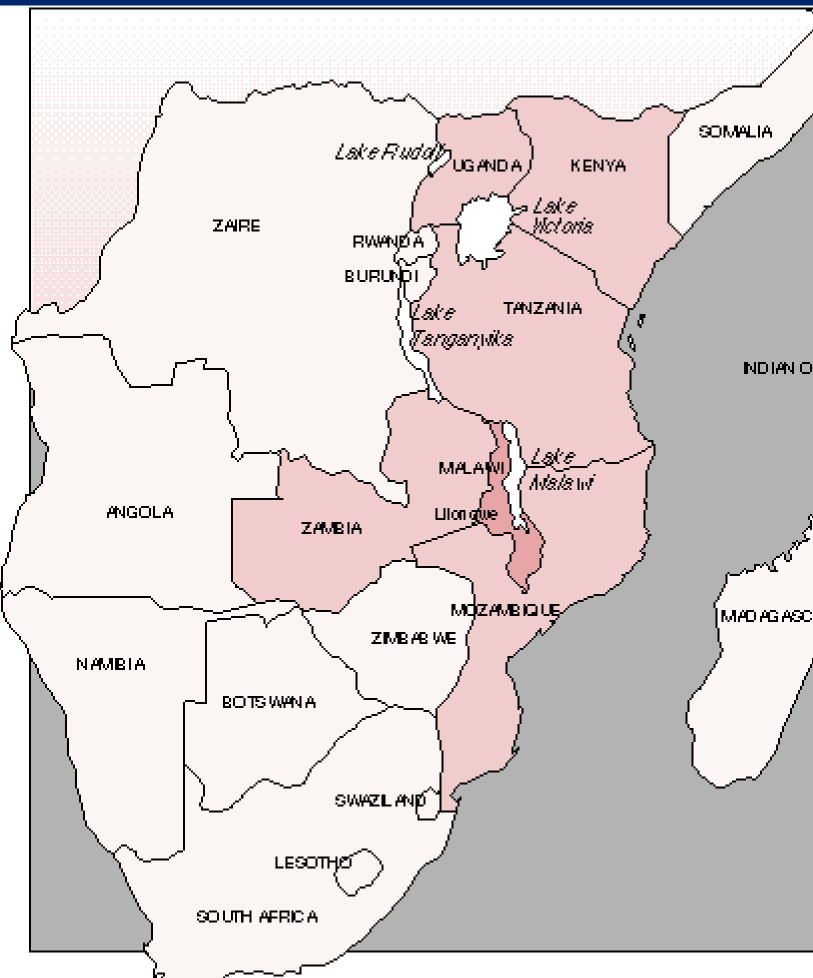
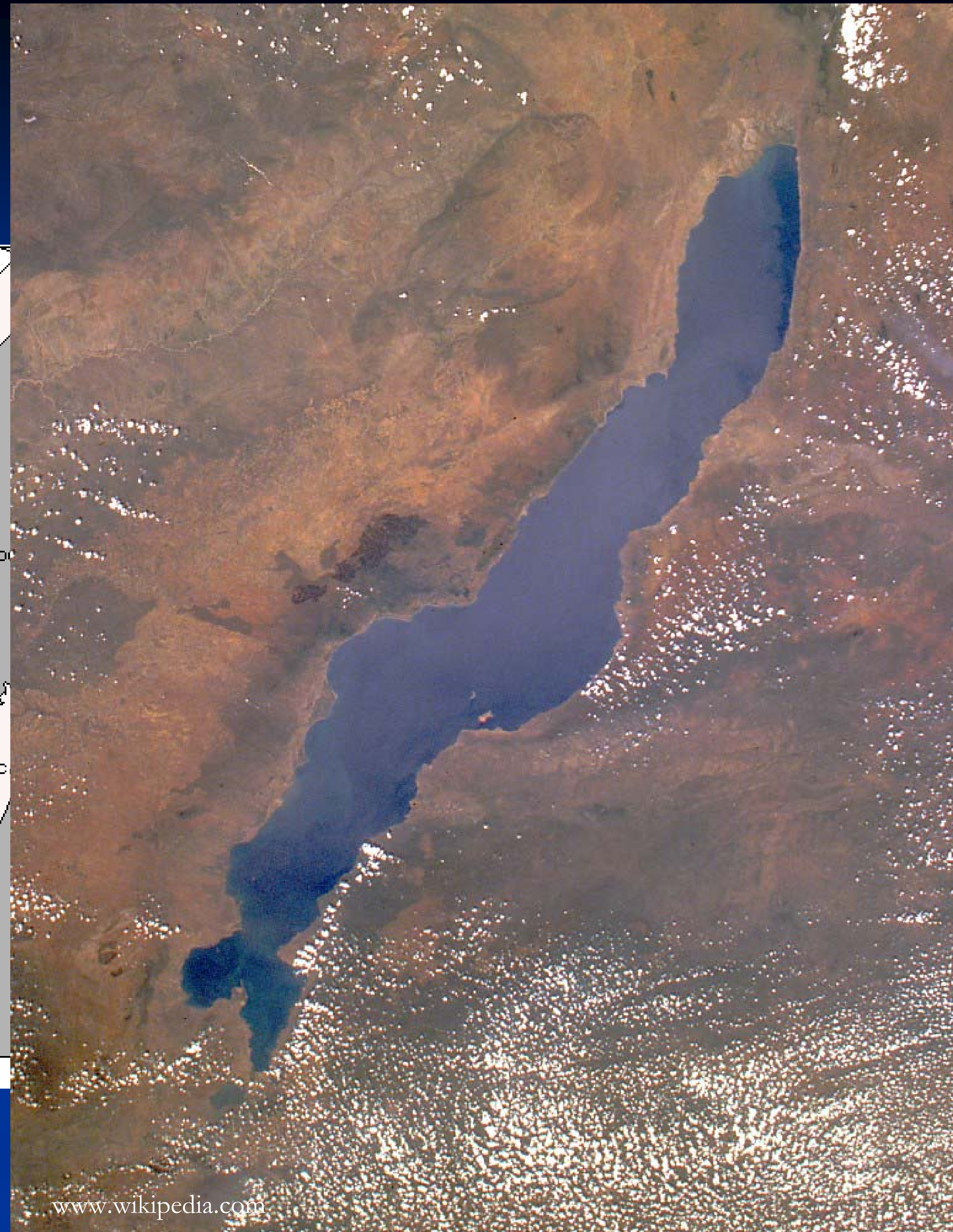
Cichlids of East Africa
A Model of Vertebrate Radiation




Lake Rudolf
UGANDA
KENYA
SOMALIA
Lake Victoria
ZAIRE
RWANDA
BURUNDI
TANZANIA
Lake Tanganyika
INDIAN OC
MALAWI
Lake Malawi
ANGOLA
ZAMBIA
Lilongwe
MOZAMBIQUE
MADAGASC
ZIMBABWE
NAMIBIA
BOTSWANA
SWAZILAND
LESOTHO
SOUTH AFRICA

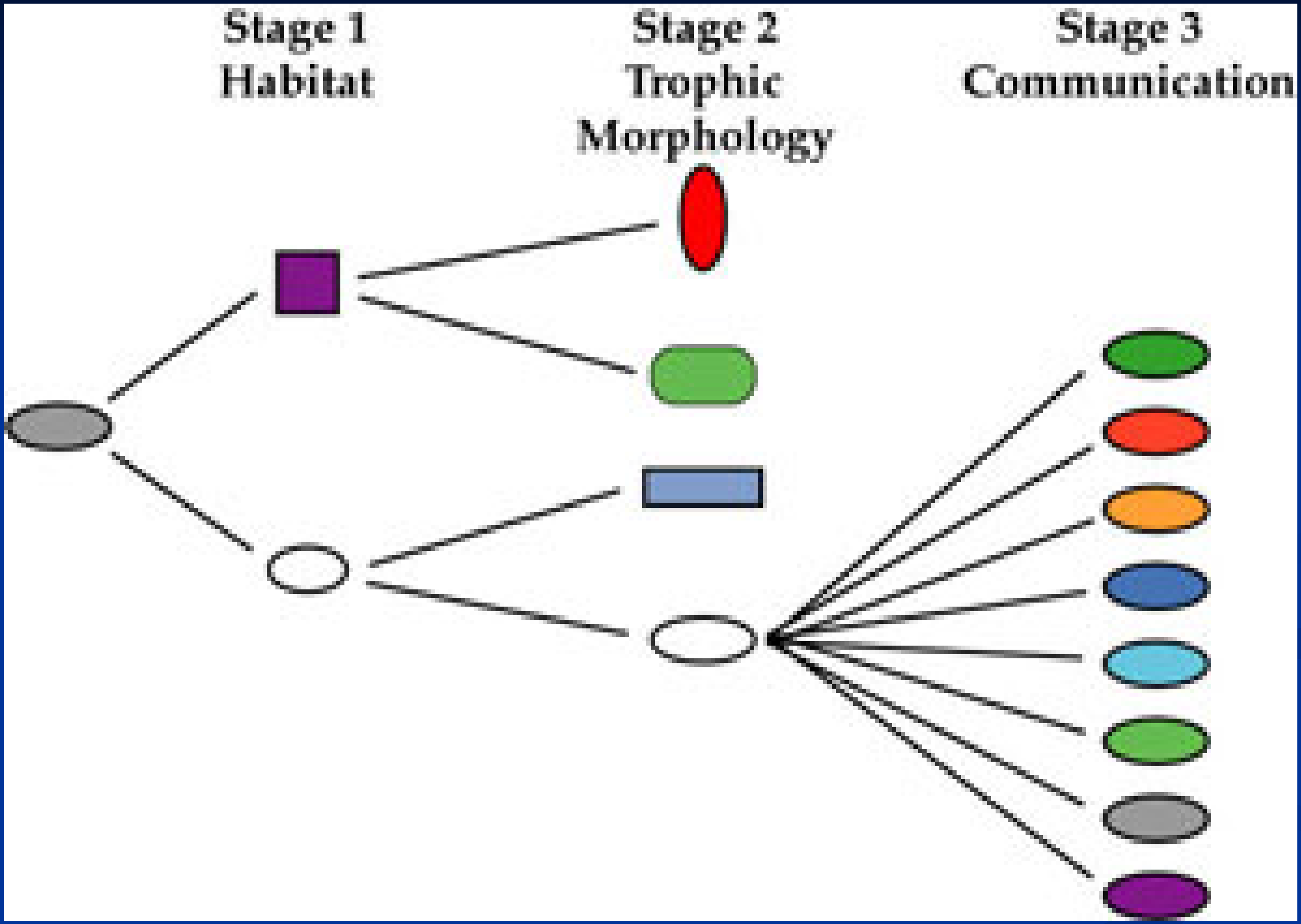

www.wikipedia.com

Lake Malawi

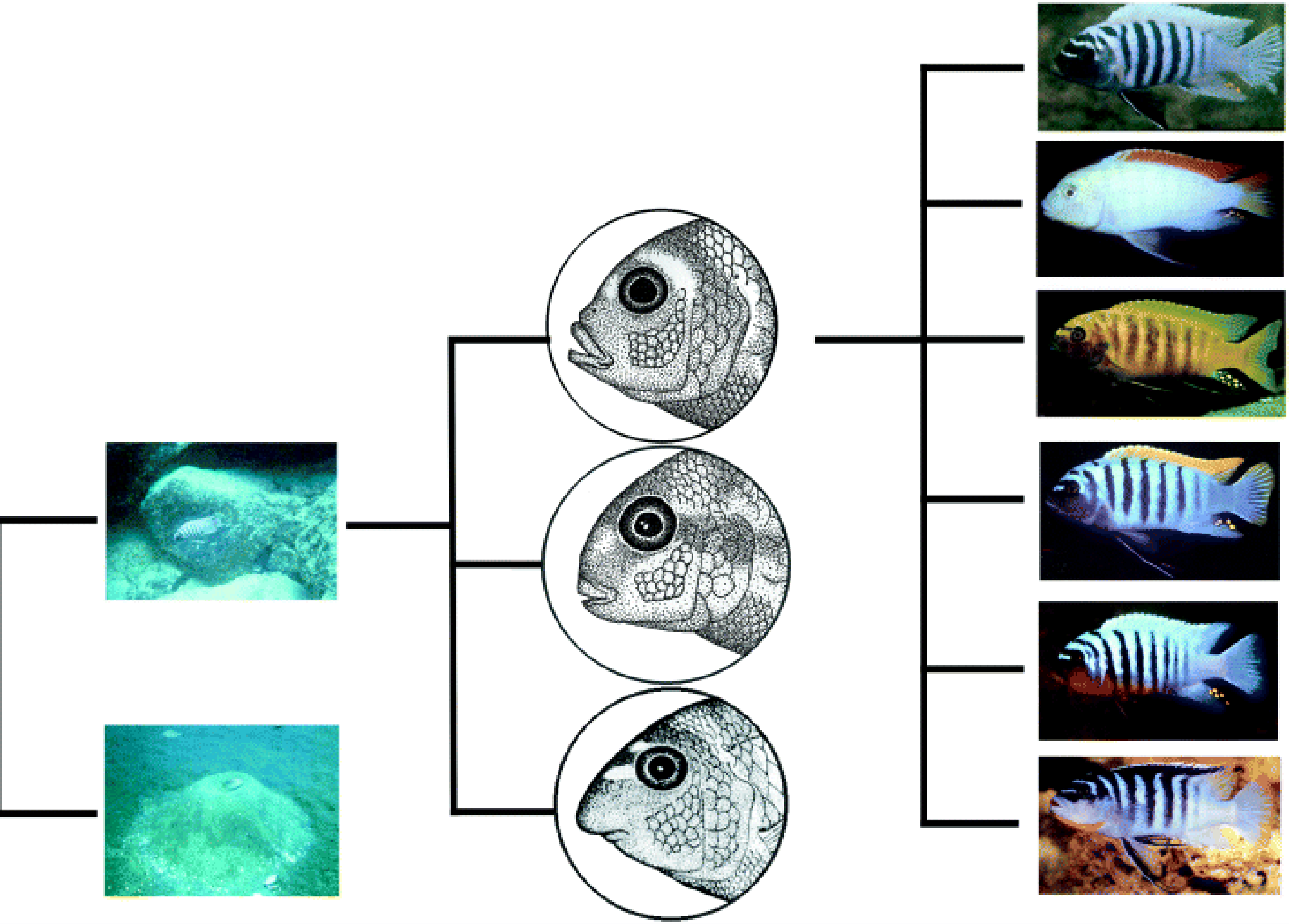
- 2-20 million years old
- Fifth largest lake in the world by volume
- Bordered by Tanzania, Mozambique and Malawi
- ~360 miles long, ~25 miles wide
- Mean Depth : 264m
- Max Depth : 706m

Cichlids of Lake Malawi

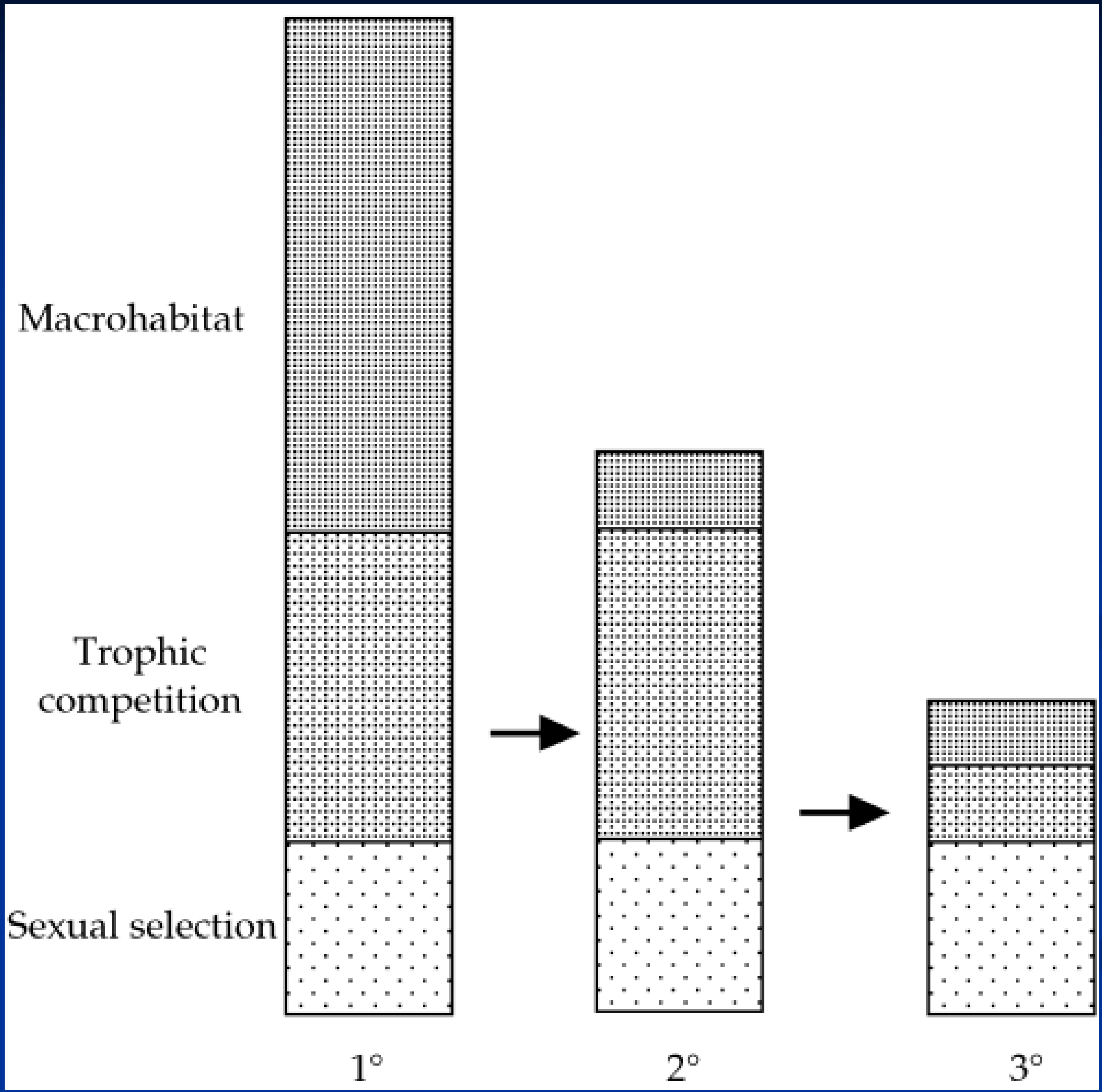
- Cichlidae family is the third largest of the teleosts
- 400-500 species are currently found in Lake Malawi
  - What is a species in Lake Malawi?
- Likely evolved in the last 700,000 to 1,000,000 years
  - A riverine ancestor
- Display remarkable diversity in trophic morphology and color patterns



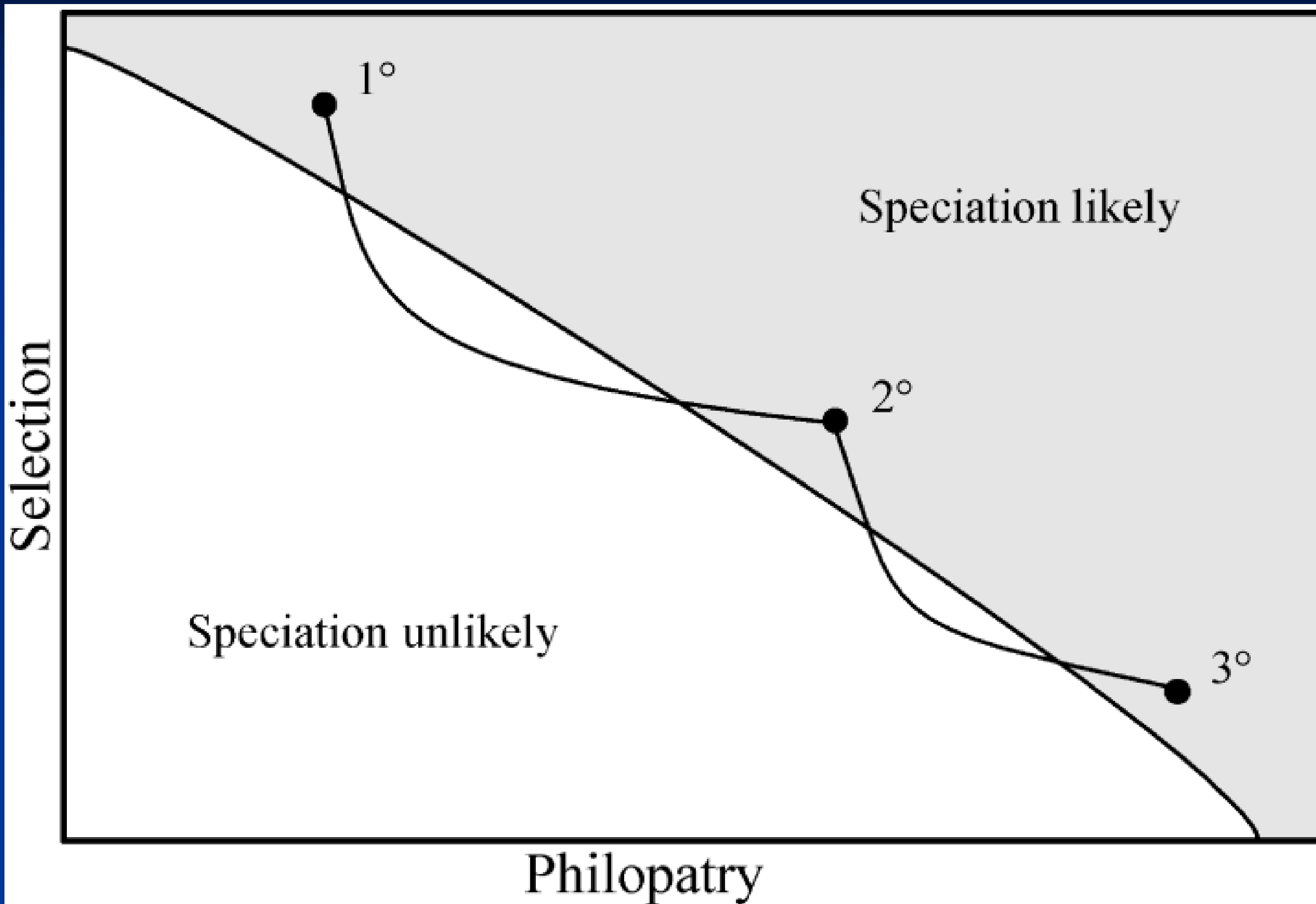
Streelman & Danley framework for vertebrate evolutionary radiations



Danley & Kocher

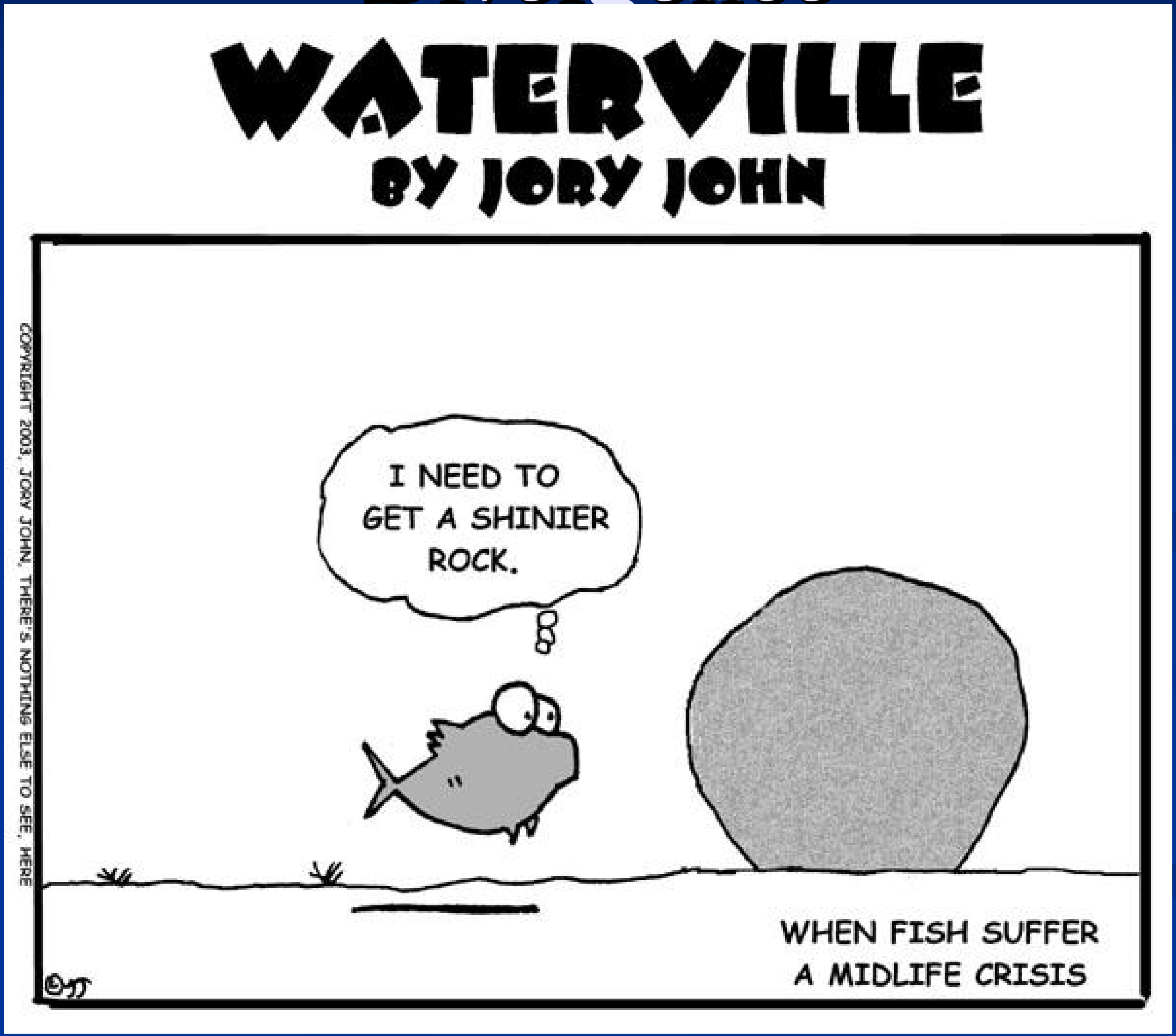


Danley & Kocher



Danley & Kocher

Primary Radiation – Habitat Divergence



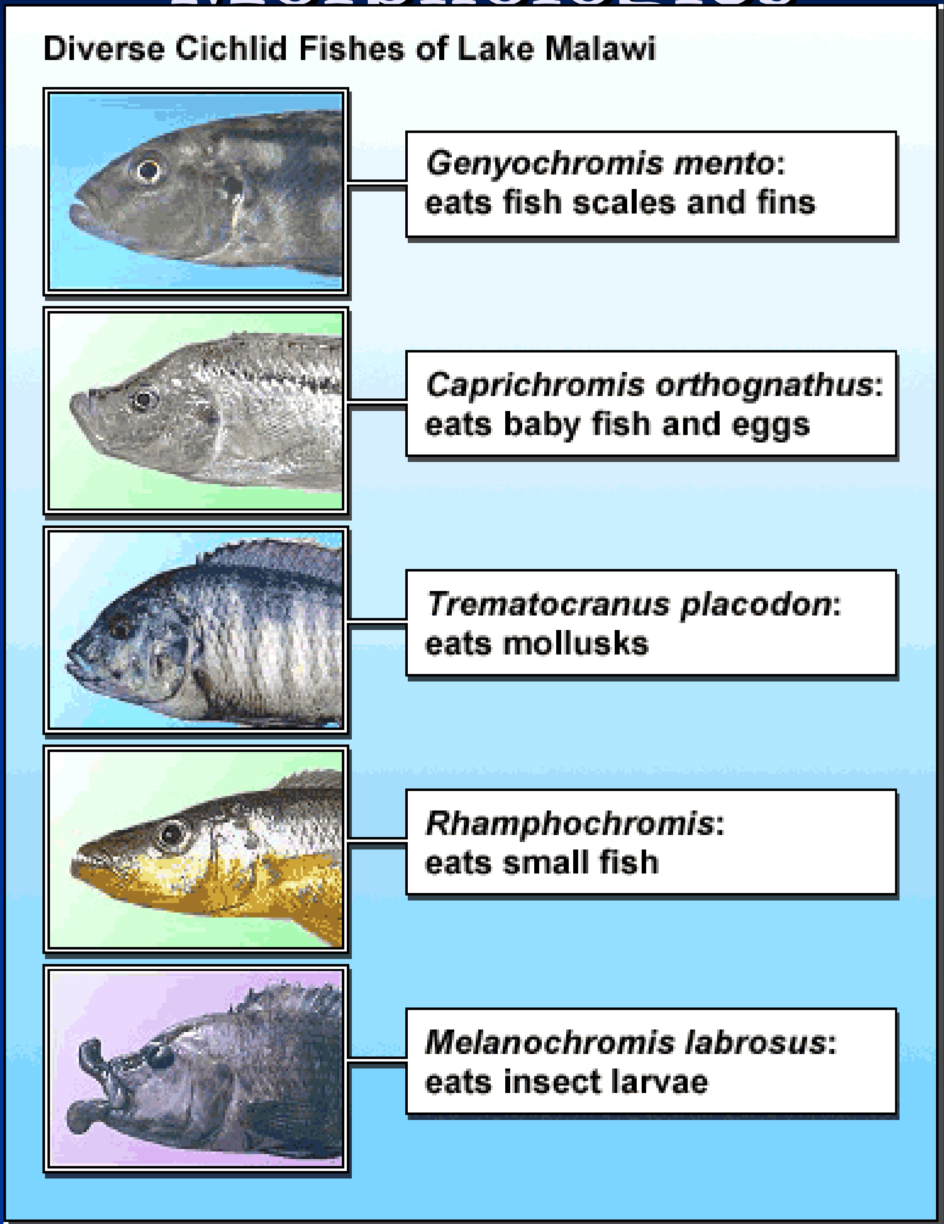
Rock / Sand

- An early generalist cichlid diverged according to the two major benthic habitats of the lake
- Members of each clade can generally be distinguished by differences in
  - Body size and shape
  - Dietary preferences
  - Chromatophore patterning
  - Reproductive behavior
  - Trophic morphology
- Primarily follows ecological selection

Other classic examples of divergence via habitat

- Sticklebacks – benthic vs. limnetic
- Marine parrotfish – reef vs. seagrass
- Galapagos finches – tree vs. ground
- Caribbean anoline lizards
  - Up to 6 ecomorphs on four islands

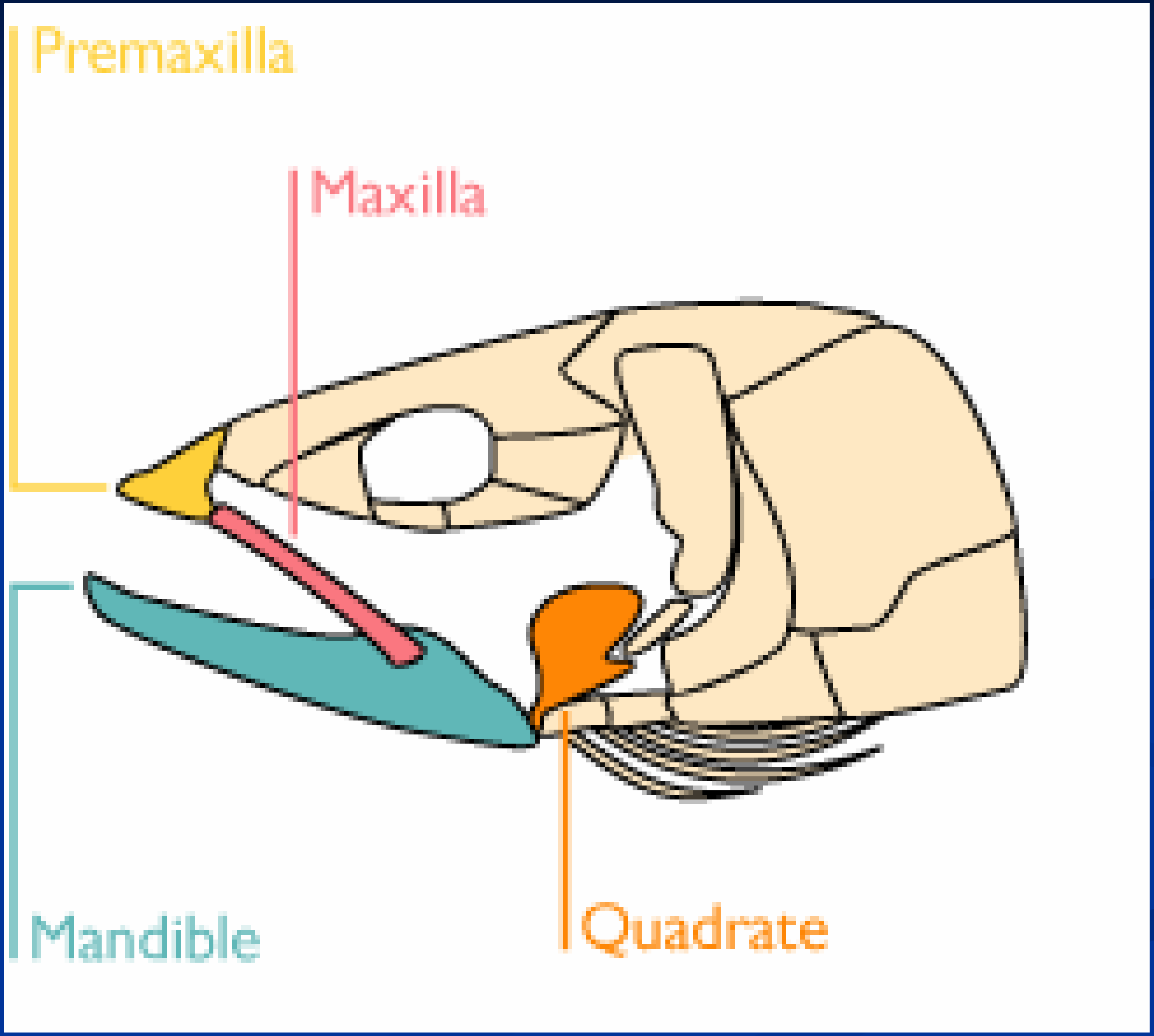
Secondary Radiation – Trophic Morphologies



www.evolution.berkeley.edu

A Novel Jaw

- Two innovations in the jaw structure of cichlids are credited with the trophic diversification
  - Pharyngeal jaw apparatus
    - In the ancestral state, pharyngeal jaws aid in the transportation of food from the oral cavity to the stomach
    - Pharyngeal teeth in cichlids play an important role in food processing, allowing oral jaw to focus on other functions, i.e. food collection
  - Decoupling of oral jaw elements
    - Kocher et al have shown that some of these elements are controlled by very few genetic factors
      - Bmp4 gene
    - Early functional divergence may have focused on three modes of feeding – biting, sucking and ramming



http://www2.biology.ualberta.ca

Cichlidae a la carte

- Fish
- Fish scales
- Fish fins
- Fish eggs
- Zooplankton
- Periphyton
- Aufwuchs
- Ectoparasites
- Mollusks
- Insect larvae

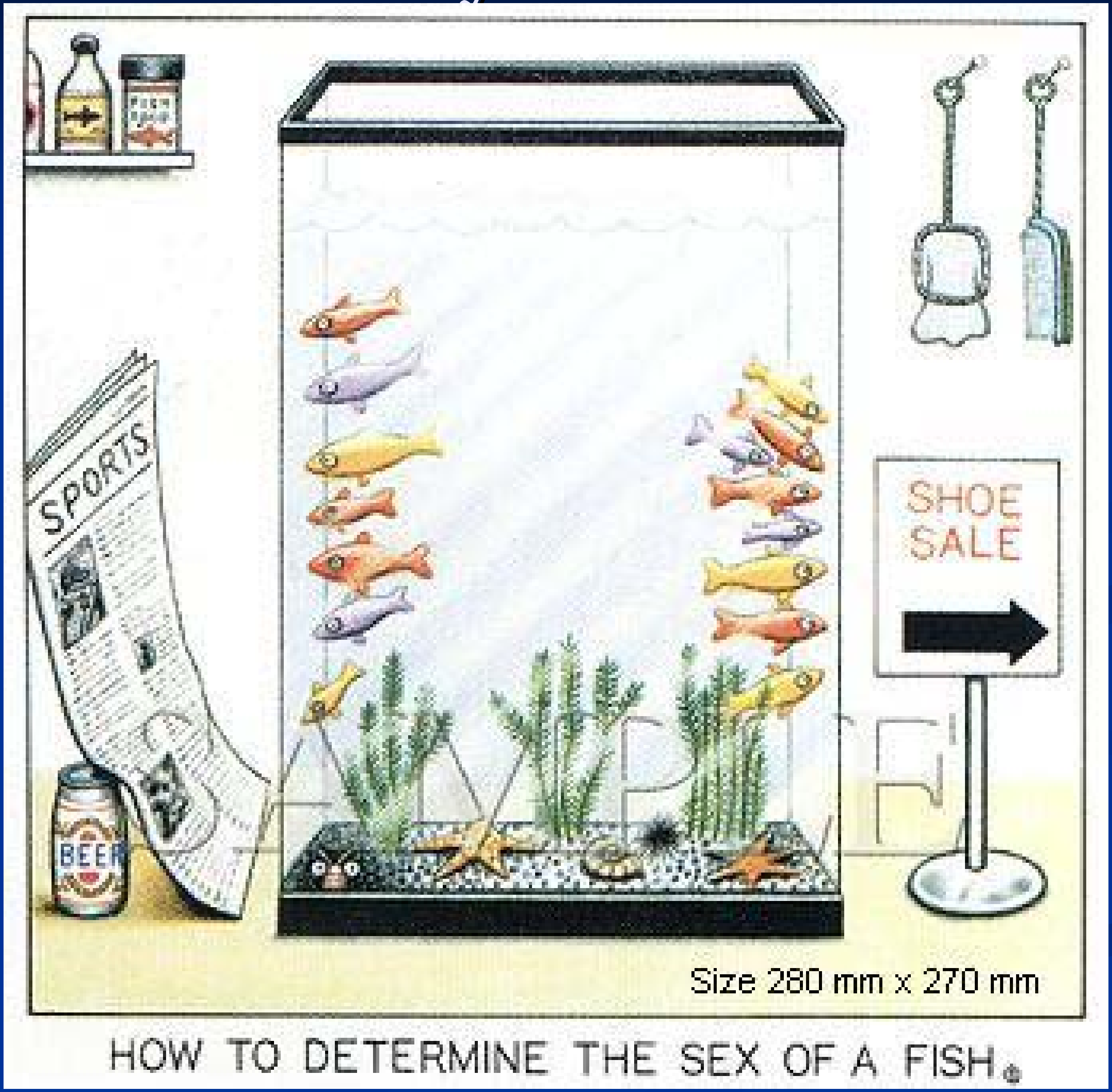
Pack your bags…

- http://malawicichlids.com/mw01100.htm

More Examples of Trophic Diversification

- Arctic charr
  - Following the benthic and limnetic divergence, the limnetic form diverged into piscivorous and planktivorous forms
- Galapagos finches
  - Beak morphologies

Tertiary Radiation

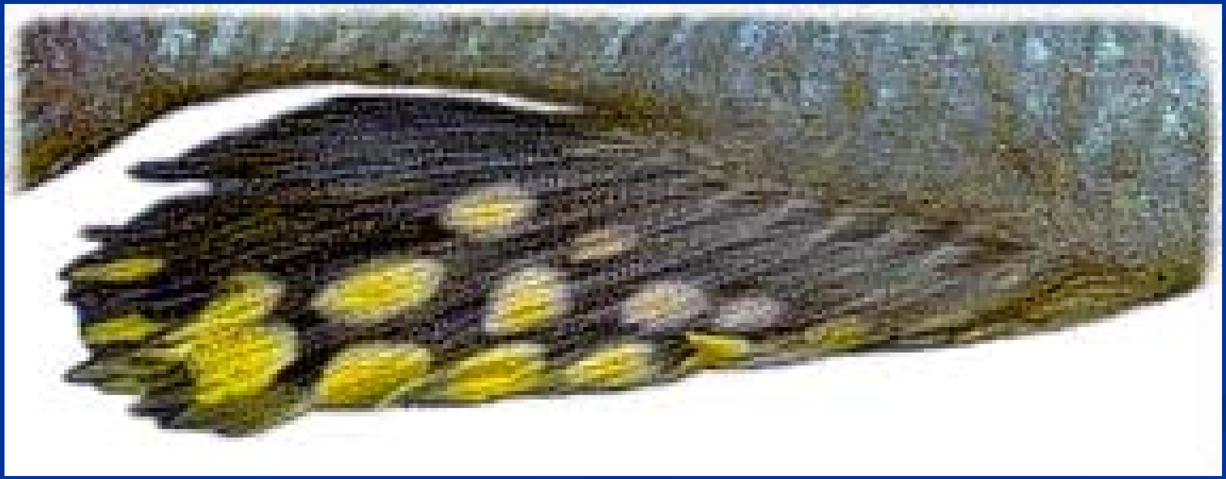


www.hug-elad.org

Sexual selection

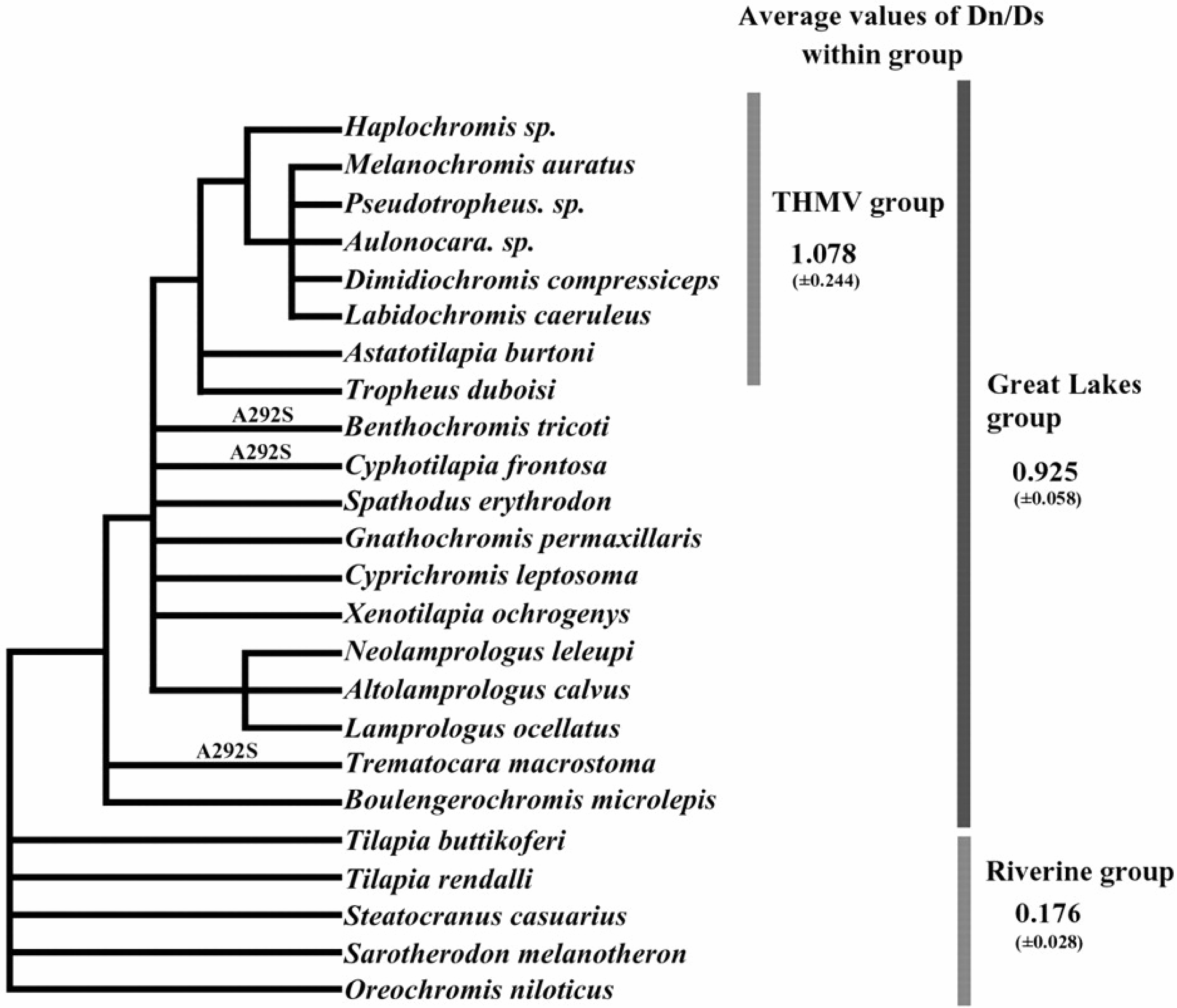
- Under the pressures of a lek-like mating system, sexual selection acts upon male coloration in most cichlid groups
- As a result, we typically see sexually dimorphic color patterns
- Variations in color patterns are not associated with macrohabitat features, unlike the stickleback and *Anolis* examples

- Nuptial coloration
  - Brighter coloration has been correlated with lower rates of parasite infestation
- Egg spots
  - Males with more egg spots on anal fin tend to have higher reproductive success

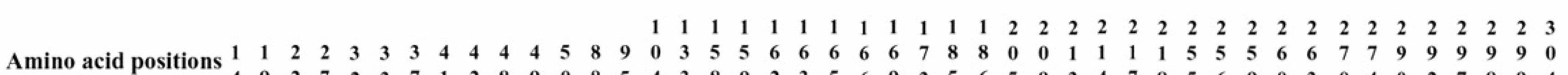


http://research.yale.edu

(a)


Average values of Dn/Ds
within group
Haplochromis sp.
Melanochromis auratus
Pseudotropheus. sp.
Aulonocara. sp.
Dimidiochromis compressiceps
Labidochromis caeruleus
Astatotilapia burtoni
Tropheus duboisi
A292S
Benthochromis tricoti
A292S
Cyphotilapia frontosa
Spathodus erythrodon
Gnathochromis permaxillaris
Cyprichromis leptosoma
Xenotilapia ochrogenys
Neolamprologus leleupi
Altolamprologus calvus
Lamprologus ocellatus
A292S
Trematocara macrostoma
Boulengerochromis microlepis
Tilapia buttikoferi
Tilapia rendalli
Steatocranus casuarius
Sarotherodon melanotheron
Oreochromis niloticus
THMV group
1.078
(±0.244)
Great Lakes group
0.925
(±0.058)
Riverine group
0.176
(±0.028)

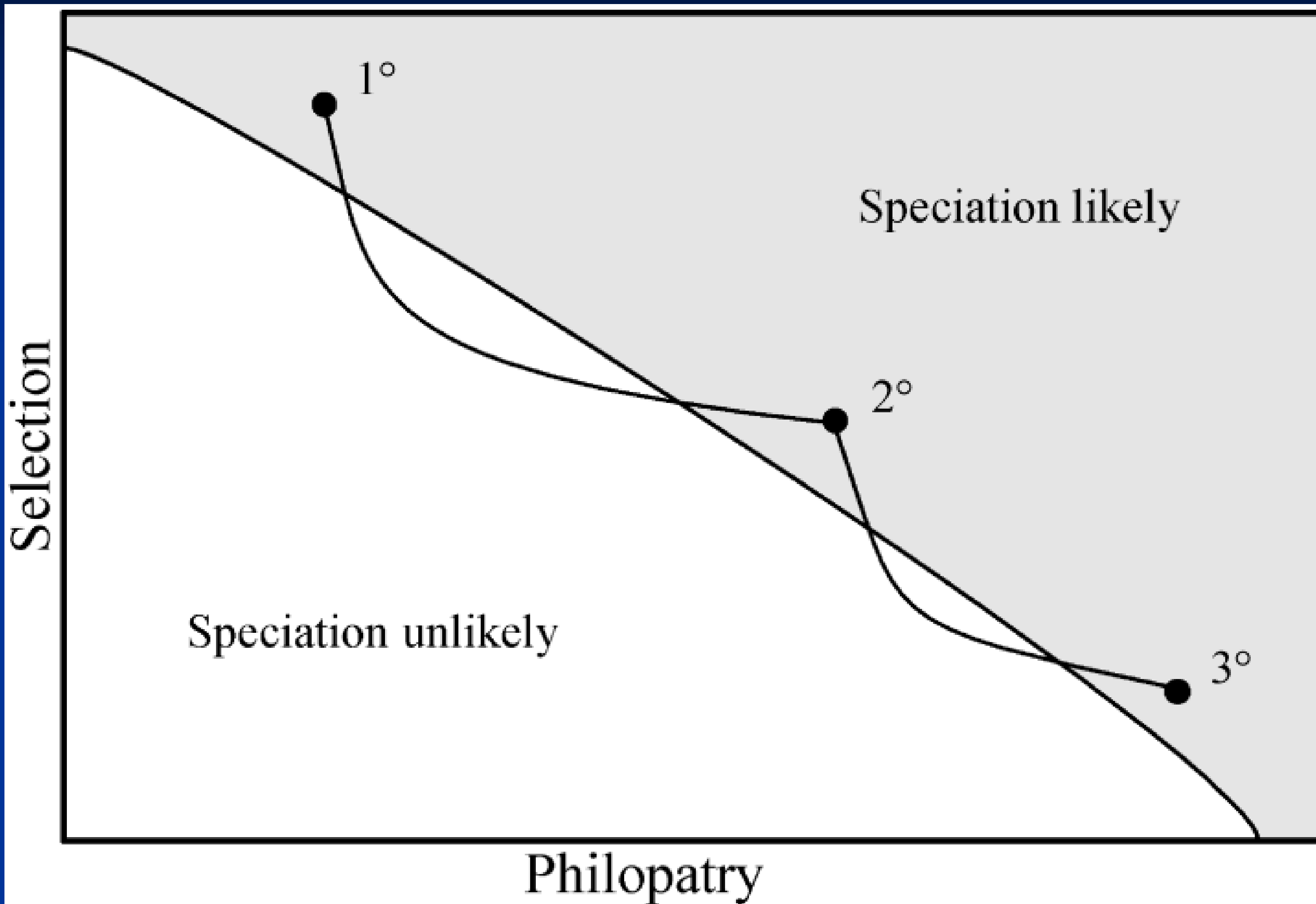
(b)


Amino acid positions

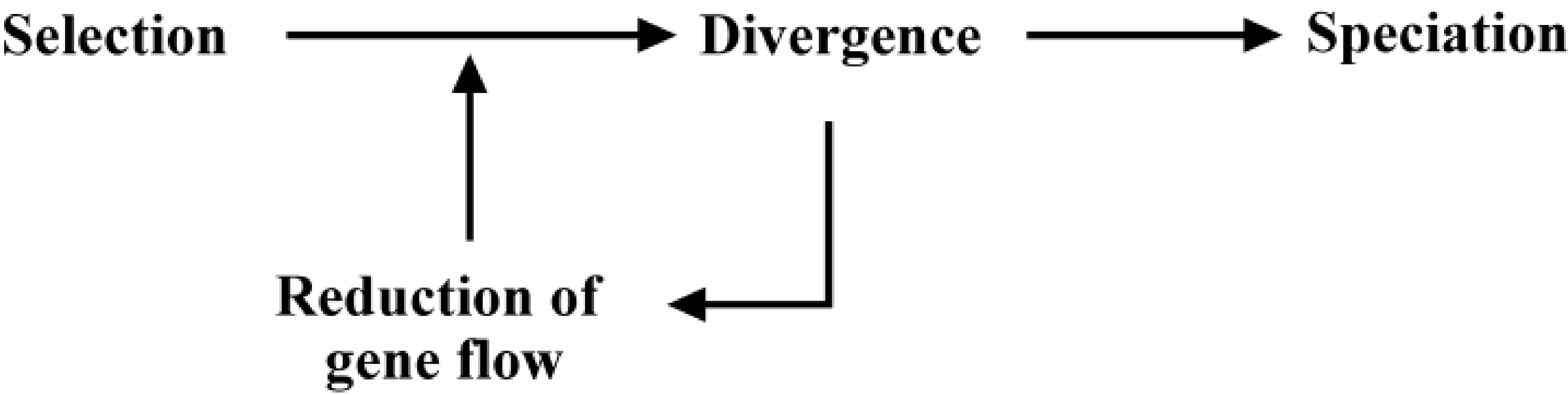
Dn/Ds

- Dn – nonsynonymous substitutions per nonsynonymous site
- Ds – synonymous substitutions per synonymous site
- Dn/Ds provides an estimate of the evolutionary rate of amino acid substitutions
- Amino acids encoded by the rhodopsin gene have evolved at an accelerated rate within cichlid lineages

- The evolutionary convergence of amino acids of the rhodopsin gene provides evidence of positive selection
- It is presumed that one substitution in particular, A292S, shifted the absorption spectra to allow some species more visual acuity in clear, deepwater habitats
- Cichlids of Lake Victoria possess 5 unique amino acid substitutions that may enhance vision in the longer wavelengths of the visible spectrum


1°
2°
3°
Speciation likely
Speciation unlikely
Selection
Philopatry

Speciation engine



Adapted from Rice and Hostert (1993)

Conservation

- Fisheries
- Pollution
- Eutrophication

References

- Albertson RC, Markert JA, Danley PD, Kocher TD (1999) Phylogeny of a rapidly evolving clade: The cichlid fishes of Lake Malawi, East Africa. *Proc. Natl. Acad. Sci.*, **96**, 5107-5110.
- Danley PD, Kocher TD (2001) Speciation in rapidly diverging systems: lessons From Lake Malawi. *Molecular Ecology*, **10**, 1075-1086.
- Streelman JT, Danley PD (2003) The stages of vertebrate evolutionary radiation. *Trends in Ecology and Evolution*, **18** (3), 126-131.
- Sugawara T, Yohey T, Norhiro O (2002) Natural selection of the rhodopsin gene during the adaptive radiation of East African Great Lakes cichlid fishes. *Molecular Biology and Evolution*, **19**, 1807-1811.